Do Only The Eyes Have It? Predicting Subsequent Memory with Simultaneous Neural and Pupillometry Data

Research Thesis

Presented in partial fulfillment of the requirements for graduation *with research distinction* in Neuroscience in the undergraduate offices of The Ohio State University

by

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Abstract

There are multiple physiological measurements that can predict successful encoding of a stimulus that can be retrieved from memory later, often referred to as a subsequent memory effects (SMEs). An event related potential (ERP) is a change in EEG signal, positive or negative, that is temporally related to an event. A late positive component (LPC), a positive signal in the parietal region, is predictive of successful memory formation (Mangels et al., 2001). A pupil response (PR) during encoding, measured as the maximum deflection in pupil size after stimulus onset, is an analogue to activity of the locus coeruleus (LC) -- a subcortical brain structure that controls the release of the neurotransmitter norepinephrine (NE)-- and also predicts successful episodic memory formation. To measure the extent to which these two potential correlates of successful memory formation overlap, we examined data from both of these sources while participants were auditorily presented with lists of common nouns, as well as when they were later tested on their recognition of those items. For ERP we found a trend towards a late positive component (LPC) in the parietal region, but it did not achieve significance. PR during encoding showed the beginning of an increase in positive response for stimuli that were later remembered, but the signal recorded did not extend the entire duration of the time period predicted for the effect and also failed to achieve significance.

Background

One goal of the field of neuroscience is understanding why we remember some things, but not others. A better understanding of what brain processes underlie accurate memory formation has ramifications not only for our daily lives, but also for afflictions like Alzheimer's disease, which impair new memory formation. Technologies like EEG and Eye-tracking have given us the opportunity to gain deeper insight into those brain processes that lead to successful memory encoding, retention, and retrieval.

EEG and Subsequent Memory Effects

Neural processes during memory encoding are that predict successful memory retrieval are know as subsequent memory effects (SMEs) (Paller & Wagner, 2002). The difference in event-related potential (ERP) between stimuli that are later remembered and forgotten is known as difference due to memory (Dm) (Paller et al., 1987). It is typically measured as a positive deflection between 400 and 800 ms in the study phase of a memory task (Paller and Wagner, 2002). However, it has also been seen as a negative deflection in the left temporal region at 200 - 300 ms (Figure 1, Mangels et al., 2001) and the size and timing of the effect vary depending on the paradigm of the experiment (Johnson, 1995).

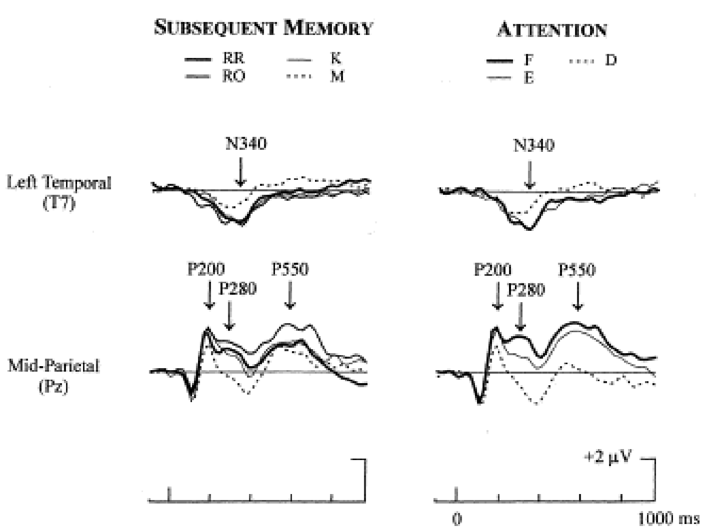

Fig. 1. Positive and negative peaks 200–800 ms after stimulus onset, shown at the left temporal (T7) and midline parietal (Pz) electrodes. ERPs were averaged as a function of subsequent memory or attention at encoding. There is a significant difference in the EEG measured cortical response to recollected items (RR and RO) as well as recognized items (K) compared to forgotten items (M)(Mangels et al., 2001).

Dm characterized by ERP has been studied in intentional learning where the participants are aware of upcoming testing (Hess & Polt, 1964; Ahern & Beatty, 1979) as well as incidental learning where participants observed stimuli unaware of the upcoming test (Paller et al., 1987). It been studied with stimulus observations that included either semantic (e.g. living or nonliving) and non-semantic (number of vowels) judgments (Paller et al., 1987). It has also been studied in connection with recall tasks as well as recognition tasks (Mangels et al., 2001).

More recent research has focused on the role of oscillations in scalp electroencephalography (EEG)(Klimesch et al., 1997; Sederberg et al., 2006) and intracranial EEG recorded in neurosurgical patients undergoing treatment for intractable epilepsy (iEEG)(Fell et al., 2001; Sederberg et al., 2003). Figure 2 shows examples of changes in oscillatory power at encoding that predict subsequent memory (Sederberg et al. 2006). Increased power and coherence of gamma oscillations (28 to 100 Hz) delocalized across many cortical regions has been implicated in successful memory formation (Fell et al., 2001; Sederberg et al., 2003; Miltner et al., 1999; Gruber et al., 2004). Decreased power of oscillations at lower frequencies (e.g., theta band [4 to 8 Hz]) during episodic encoding may also play a role in successful memory formation (Sederberg et al., 2006). Additionally, increased coherence in oscillation between frontal and posterior scalp electrode sites, as well as significant increases in 1 to 4 Hz power, predicted subsequent recall for visually and auditorily presented nouns (Weiss & Rappelsberger, 2000).

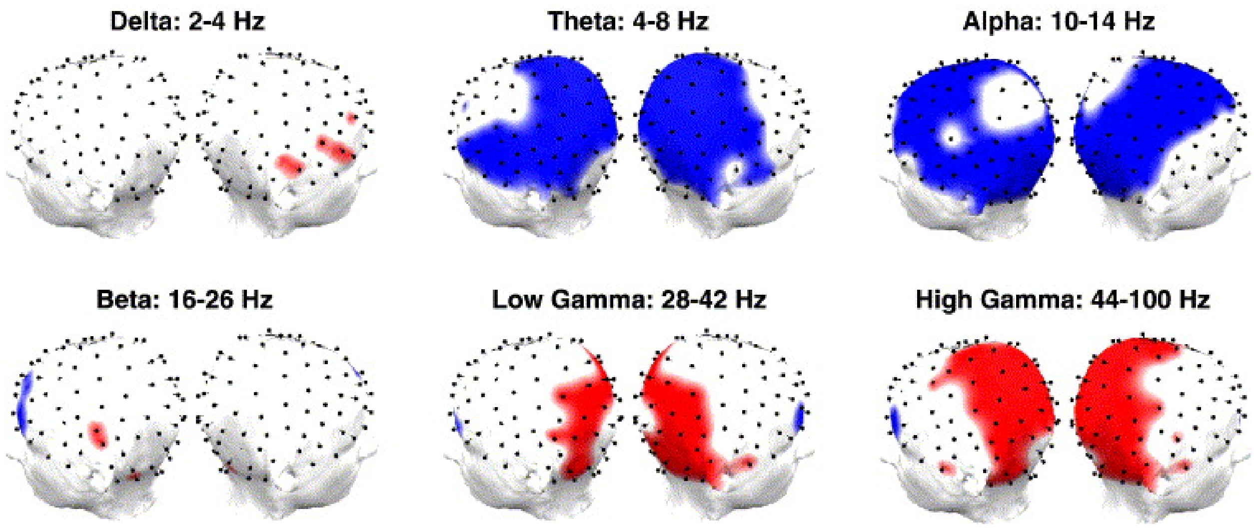

Fig. 2. Topography of significant subsequent memory effects for items from both early and middle serial positions. Each pair of scalp topographies illustrates the electrodes exhibiting significant increases (red) or decreases (blue) in power during encoding that predicted successful retrieval for six distinct frequency bands (Sederberg et al. 2006)

Pupillometry

Changes in pupil diameter (pupillometry) have also been studied as correlates of underlying neural processes with changes in pupil diameter ranging up to ~ 0.5 mm (Beatty & Lucero-Wagoner, 2000). Pupil diameter has been shown to track positively with increasing loads on working memory (Beatty & Kahneman, 1966), increasing difficulty of mental calculations (Hess & Polt, 1964; Ahern & Beatty, 1979) and other approximations of executive load or working memory load (Chatham, Frank, & Munakata, 2009; Hyönä, Tommola, & Alaja, 1995). Very recently Hoffing & Seitz (2015) have generated strong evidence that 'pupil size changes (PSCs)' are an accurate predictor of human memory encoding.

The reason that PR correlates with cognitive load and successful memory encoding is because it is partially controlled by the activity of the Locus Coeruleus (LC)(Samuels &

Szabadi, 2008). The LC is a subcortical brain structure found in the brainstem on either side of the rostral end of the pons, that is the sole source of the neuro-transmitter norepinephrine (NE) to the cortex, cerebellum, and hippocampus (Aston-Jones & Cohen, 2005; Sara, 2009). The LC releases NE as part of the stress response as well as during the process of memory retrieval (Sterpenich et al., 2006), the latter suggesting that it plays a role in memory consolidation. Current hypotheses suggest that the LC-NE system mediates the integration of the attention system which may contribute to its role in memory encoding (Corbetta, Patel, & Shulman, 2008; Coull, Büchel, Friston, & Frith, 1999; Hoffing & Seitz, 2015; Sara, 2009).

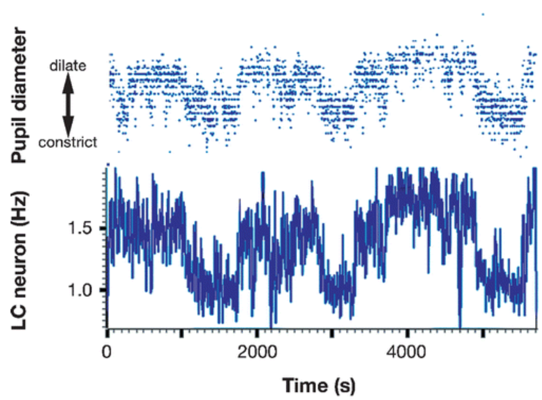

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Fig. 3. The top curve shows pupil diameters as taken by a remote eyetracking camera while a monkey fixated on a spot of light during a signal detection task. The bottom curve displays the baseline firing rate of an LC neuron while it was recorded from an electrode at the same time as the pupillary responses. The two measurements are shown to be phased-locked to one another (Aston-Jones & Cohen, 2005).

Figure 3, made using single-cell recording in monkeys, shows that PR is phase-locked --nearly perfectly correlated-- to changes in the baseline activity of neurons in the LC (Aston-Jones & Cohen, 2005). In the past, these animal models were the source of the most compelling evidence for PR coupling with LC-NE activity (Aston-Jones, 2005;

Rajkowski, Kubiak, & Aston-Jones, 1993). However, more recent studies in humans have shown PRs that were positively associated with learning rate (Silvetti, Seurinck, van Bochove, & Verguts, 2013; Nassar et al., 2012) and increased task performance (Murphy, Robertson, Balsters, & O'Connell, 2011). Hoffing & Seitz (2015) showed that induced LC-NE activity (by presentation of an unexpected noise) generates a PR and leads to better memory encoding as well. These studies provide evidence that PRs are related to learning supports the hypothesis that the LC-NE system has a role in driving both pupil size changes and learning.

Introduction

This experiment sought to answer the question of whether or not pupil response (PR)-based prediction of subsequent memory coincides with EEG-based prediction of subsequent memory, event-related potentials (ERPs). If they are mutually predictive, then it would follow that both can be used as measurements of the same memory encoding process, allowing future researchers more options in studying human learning and memory.

The design of this study was an incidental memory paradigm in which the participants were presented with lists of auditory words and were unaware that they would later be tested on their memory of those words. During the study phase, the participants made a non-semantic judgement about the words which will hereby be referred to as the alphabet task; they were instructed to press the letter 'J' on the keyboard if the first letter was in the first half of the alphabet, or to press the letter 'K' if it was in the second half. The use of recognition memory and low levels of semantic processing is important because it is reflective of a large part of how people experience the world, unintentionally and without deep levels of thought. Auditory presentation is being used to isolate the effect of attention and LC activity on the control of the pupil. Visual stimuli present several problems for this kind of study. Uneven luminescence and complexity can affect pupil diameter because of shifting attention to different details of the image. Even when every other problem with visual stimuli are addressed, it remains impossible to tell for certain if the pupil response is solely from underlying activity of the LC, or if it due to some other aspect of visual processing.

Methods

Participants. 10 right-handed volunteers (7 female) with self-reported normal hearing and normal or corrected to normal vision were recruited via flyers posted around The Ohio State University. Participants were undergraduate students enrolled in Ohio State University of at least 18 years of age. They were compensated 20 USD for their participation. All participants provided consent in accordance with the requirements of the OSU Institutional Review Board.

Exclusions. 3 participants were excluded (2 female) . 2 due to incompletion of experiment and 1 due to excessive noise in the EEG data. Of the 7 remaining participants 5 were female.

Materials and Measures. 480 emotionally neutral auditory nouns were selected from the Auditory Toronto Word Pool.

EEG data was collected constantly throughout the experiment using 64 electrodes placed around the scalp with a small amount of saline gel at each electrode to reduce impedance. A wavelet-enhanced independent components analysis algorithm corrected for eyeblink and motion artifacts (>60 μV) without having to reject events due to movement or muscle interference (Castellanos & Makarov, 2006). EEG data were aligned to each behavioral trial using time-stamped sync pulses sent to the EEG recorder at the beginning of each trial.

Eye movement and pupil diameter data was collected with an EyeLink 1000 desktop eye tracker (SR Research, 2010) at a sampling rate of 1000 Hz. The tracking mode was set to “pupil only,” and the eye-to-track parameter to “Right.” Pupil area was measured using centroid mode throughout the study. Centroid mode computes pupil area using a center-of-mass algorithm that identifies the number of black pixels (SR Research, 2010). Each participant was seated on a comfortable chair with their head supported by a chinrest to minimize movement. Eye-tracking data was collected during encoding and retrieval from stimulus onset until the participant responded. Blinks caused gaps in data that had to be averaged over using univariate spline interpolation. Univariate spline interpolation is as algorithm that draws a smooth curve between data points. Trials with double blinks and other artifacts that couldn’t be corrected for by spline interpolation were excluded from further analysis.

Procedure. The experiment had 1 practice study block followed by 10 study blocks and then 10 test blocks. Each study list consisted of 20 words randomly selected from the pool without replacement. Each test list included all 20 words that were in the corresponding study list as well as an additional 20 novel words (lures) also selected from the word pool that were not used in any study list. The practice block was a study block with 10 words that were not used in any other block. Participants were unaware that there would be any test prior to the beginning of the test blocks. At the beginning of the experiment, participants completed a 9 point calibration with the eye-tracker. At the beginning of each block, study and test, participants performed a drift correction task where they fixated on a fixation cross "+". The experimenter would confirm for the computer that the fixation was being made, and then the eye-tracker would correct for any misalignment that had occurred since calibration.

Study Phase. For each study block, a list of 20 study words were presented auditorily one at a time. Participants were instructed to fixate on a fixation cross "+" in the middle of the screen that remained present throughout the course of the entire block. To ensure an even level of attention to each stimulus in the study blocks, they performed the alphabet task described above. They were informed that the instructions would not be present on the screen during the task and were asked to commit the instructions to memory. Instructions were not present on the screen during any task because of the significant EEG signal created when participants look at the answer choice they are going to select. They were given 2 seconds to make a response. If no response was made in time, the trial was marked incorrect and the experiment proceeded to the 1500 - 2500 millisecond interstimulus interval (ISI) that followed each stimulus. The ISI decorrelated the physiological responses from successive word presentations. After each block the participants were given a reminder of the instructions as well as feedback on their performance to provide them motivation to perform well on the task. At the beginning of the study phase, participants performed a practice study block with 10 items not used in any other study or test block.

Test Phase. After hearing all 10 study lists, the participants were given instructions for and then performed an item recognition task. For each word, the participants were instructed to judge if the word is 'new' or 'old', and to rate their confidence in that judgement using 4 keys: 'J', 'K', 'L', and '; (semi-colon)'. For half of the participants the keys were assigned: 'J' Sure Old, 'K' Maybe Old, 'L' Maybe New, ';' Sure New. For the other half of the participants the responses were mapped to the keys in reverse order: 'J' Sure New, 'K' Maybe New, 'L' Maybe Old, ';' Sure Old.

Results.

Behavioral.

Mean hit rate across participants was 70.8% and false alarm rate was 40.2% with d' values ranging from 0.3 to 1.3. D' is a measure of sensitivity that accounts for hits and false alarms-- a d'of 0 means there is no discrimination between signal and noise. Reaction times (RT) were calculated separately for study and test, and trials with extreme values were excluded from further analyses. The threshold for outliers was calculated by multiplying the interquartile range by 3 and adding that to the value for the 75th percentile. Mean performance at study was 97.4% with a standard deviation of .16, showing that participants were fully engaged with the study task.

EEG.

Figure 4 is the comparison between targets that were answered correctly (Hits) against targets that were answered incorrectly (Misses) at 700ms we found a negative ERP in the right frontal region (electrode FT10) and a positive ERP in the left parietal/occipital region (electrode PO3). 700 ms was chosen because it is consistent with the anticipated time range for a LPC found in previous ERP studies, 400 - 800 ms. PO3 was at the center of the greatest positive effect in that time range and was therefore used for the comparison. Despite following the anticipated trend, the difference in both regions did not reach the level of significance.

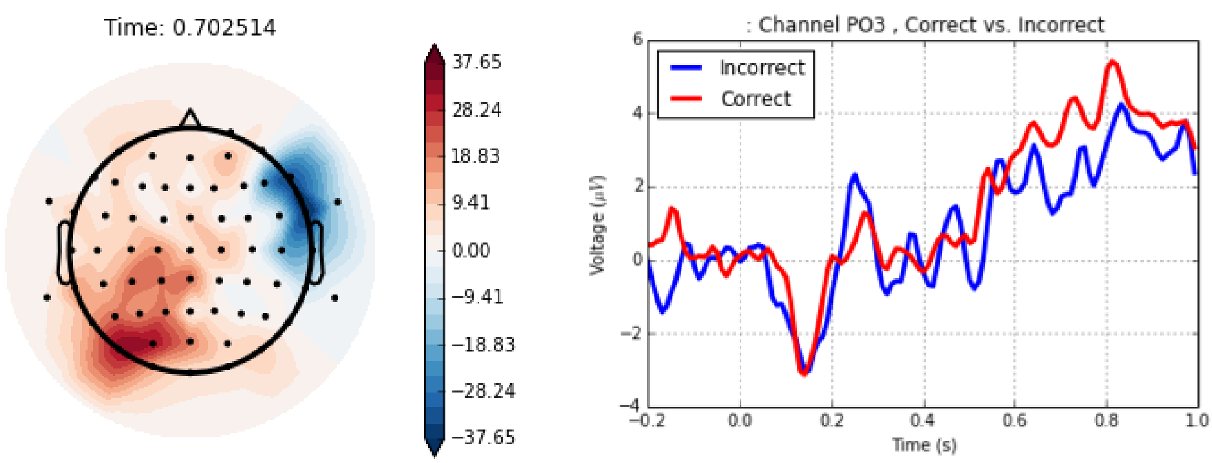

Fig. 4., comparison of ERPs at 700ms after stimulus onset of targets that were later correctly identified (Hits) against targets that were later incorrectly identified (Misses). Hits showed a weak increase in power (μV) in the left parieto-occipital area (PO3), as well as a decrease in relative power in the frontotemporal region (FT8).

Figure 5 shows the difference in activation between confident hits and lures during the test phase. The confident hits show a similar, stronger, trend towards a positive increase in activation in the parietal region (Pz) at 650 ms. The timing and position of the electrode was chosen for the same reason as for the other result, 400 - 800 ms is the expected time for an encoding effect in EEG data, and the parietal region (Pz) is the center

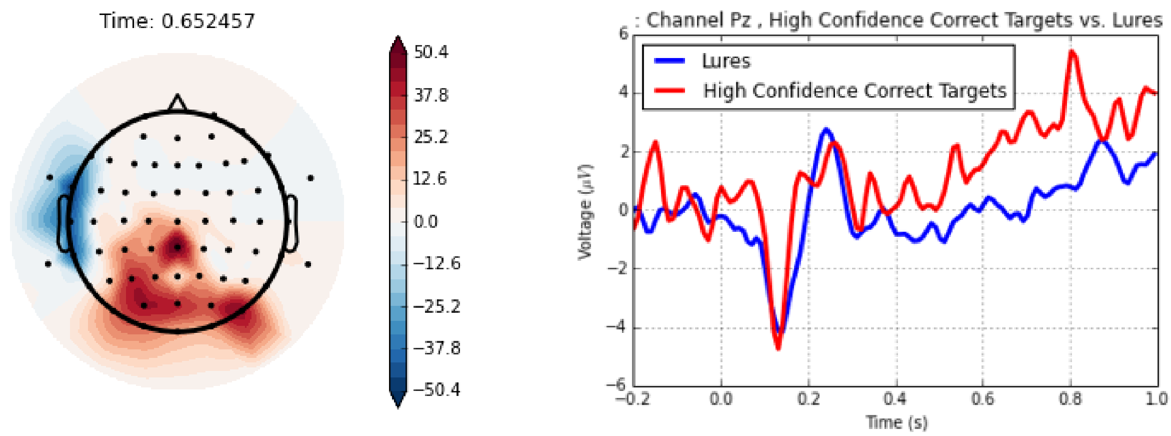

Fig. 5., ERP at 650ms during test of Confident Hits compared to all lures in the parietal area (Pz). There is a trend towards an LPC that shows a stronger activation for objects that have a relatively strong memory trace to retrieve compared to lures which have no memory trace.

Pupillometry.

PR was averaged trials within participants and then across participant, shown in Figure 6. Data was only considered for time points where there was data for every participant for every trial. Including the additional data where only some participants and trials had values resulted in large amounts of noise. Recording begins at stimulus onset, and all time points before 400 ms can be disregarded as noise because that is too fast for any kind of pupillary response to take place. The difference at was not significant (p-value = 0.0653) but shows a very strong trend.

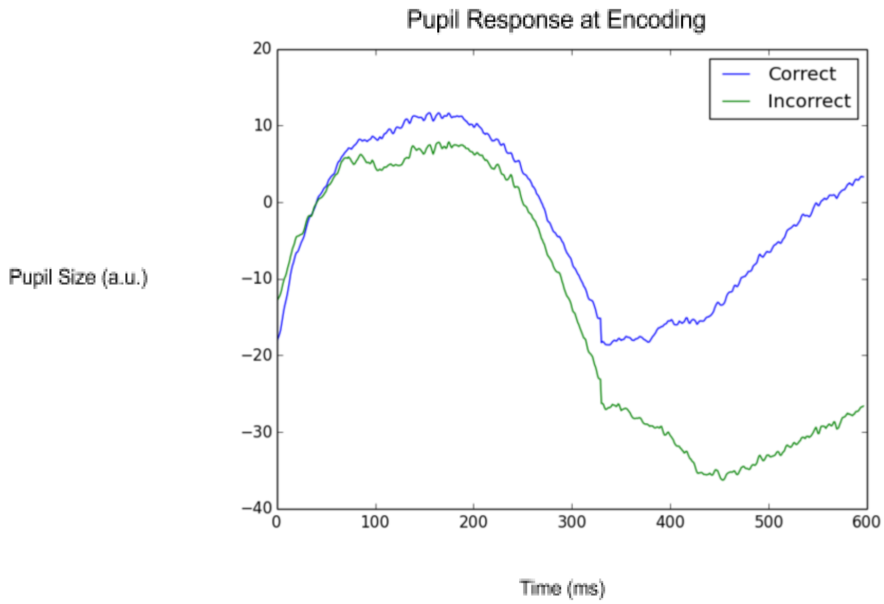

Fig 6., average pupil size across subjects as a function of time for remembered and not remember stimuli.

Discussion.

This experiment studied the difference in memory (Dm) for items that can be predicted by event related potentials (ERPs) and pupil responses (PRs) that follow the onset of auditorily presented stimuli.

Figure 4 presents a comparison between targets that were answered correctly (Hits) against targets that were answered incorrectly (Misses) at 700ms the positive ERP in the left parietal/occipital region (electrode PO3) trends towards the late positive component (LPC) found at around 400 - 800 ms in previous studies (Paller et al., 1987; Mangels et al., 2001). The result is more lateralized than expected and much weaker--not at the level of significance. The difference in power observed is explained by the paradigm used in the design of the experiment. The non-semantic judgement encoded very weak memory traces that are often difficult to observe and inconsistent (Knehans et al., 1993).

Recognition tasks also show a weaker SME compared to recall tasks because recall tasks only show the more strongly encoded targets (Paller et al., 1988).

The comparison in Figure 5 looks at the difference in activation between confident hits and lures during the test phase. The confident hits show a similar, stronger, trend towards a positive increase in activation in the parietal region (Pz) at 700 ms. This effect mimics the LPC effect we expected to see at encoding for items that were successfully recalled. It is possible that a some kind of re-encoding process is taking place in that region when the stimuli with strong memory traces are retrieved.

The PR shown in Figure 6 is the beginning of an increase in diameter following the encoding of objects that were later remembered. Although the effect does not obtain significance, it follows the expected trend supported by current research (Hoffing & Seitz, 2015). Increase in pupil diameter at encoding indicates an upregulation in the activity of the LC-NE system (Aston-Jones, 2005) which corresponds to increases in attention, arousal, cognitive load, and human memory encoding (Corbetta, Patel, & Shulman, 2008; yönä, Tommola, & Alaja, 1995; Hoffing & Seitz, 2015). The greater increase in diameter for objects that were correctly remembered supports the hypothesis that LC-NE activity is predictive of successful memory encoding and can be measured by a positive PR following encoding.

The fact that the PR was near significance, but the EEG signal wasn't is puzzling. Based on current research, we expected to find a positive EEG signal in the parietal area at 400 - 800 ms that was predictive of memory, but that result was very weak. We then expected to find a PR that peaks at 1500 - 2000 ms, which it appears we saw the beginning of, that was also predictive of memory. The hypothesis is that stimulus presentation leads to some activity in the brain whereby that stimulus is encoded into memory. LC-NE activity is implicated because it corresponds to cognitive load and is upregulated, reliably measured by PR, during trials that are remembered. That LC-NE activity may be connected to activity in the parietal lobe, part of the sensory processing region of the cortex, because activity in that area, measures as ERPs by EEG, has also been shown to be predictive of memory. It is unclear why we found a PR but not an ERP. It could be the case that the number of participants was simply too low to have sufficient power. It may also be that PR is a more sensitive measurement than ERP for the very low levels of processing induced by this experimental paradigm.

Limitations

A significant limitation of the study was the use of a non-semantic judgements task at study lowered the amount of processing that subjects were required to do during study, which likely resulted in a much weaker memory for the object. This would explain why there was a trend towards the LPC, but it did not reach the level of significance. In a future study, a semantic judgement during study, such as "living or non-living" would involve deeper processing and lead to a stronger memory trace and a stronger ERP.

Another limitation of the study is the duration of time that the eye-tracker was set to record pupil diameter. PR is a relatively slow process that takes upwards of 2 seconds post-stimulus onset to reach its maximum deflection from baseline. Extending pupil recording to last the entire duration of the ISI would give a signal that lasts through the entire time period that a PR would be expected to be, and show a larger maximum difference. Also, participants blinks caused gaps in pupil Giving participants specific instructions to minimize the amount they blink after stimulus onset may have given a better signal to noise ratio in the pupillometry data.

Future Directions

Oscillatory power analyses could provide additional insight into possible SMEs that aren't seen in ERPs. Both intracranial and scalp EEG studies have demonstrated that oscillatory activity, especially in the gamma band (28 to 100 Hz), can differentiate successful and unsuccessful episodic encoding (Sederberg at al., 2003). Oscillatory analysis is a complementary approach to the question of what brain processes are directly involved in the encoding of an event alongside ERP analysis.

Another possible future direction is the use a learning paradigm with a greater likelihood to give a strong signal. This would be better for establishing the relationship between PR and ERP. Testing could be done using intentional learning paradigms and with a recall task in addition to or instead of the recognition task.

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Appendix

Fig. 1 - Negative ERP that Predicts Item Recognition

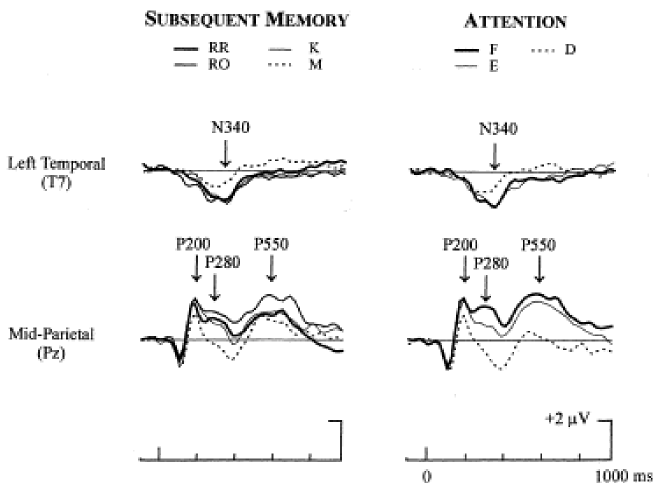

Fig. 2 - Change in Oscillatory Power of Frequency Bands that Predicts SMEs

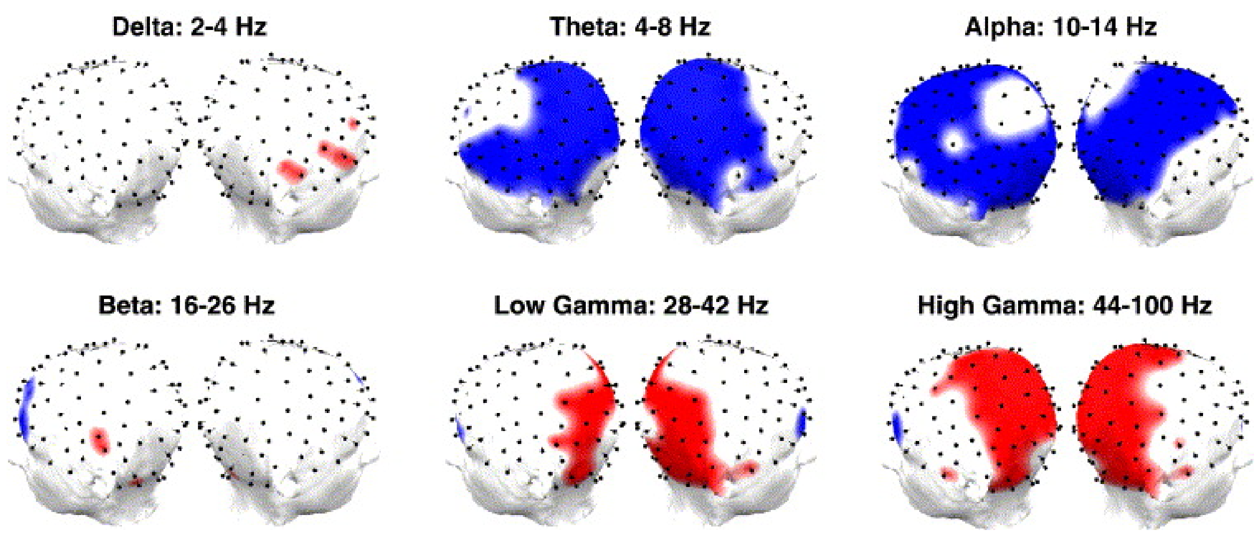

Fig. 3 - Phase-Locking of Pupil Diameter with Locus Coeruleus Activity

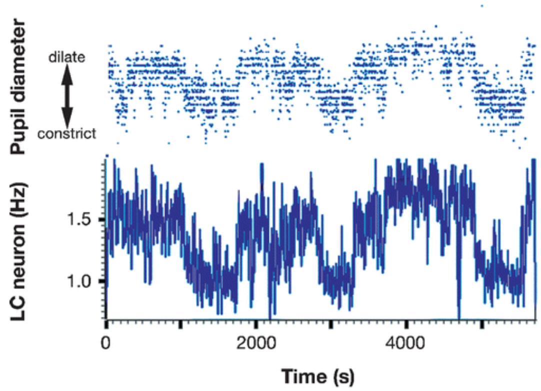

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Fig. 4 - ERP at Encoding of Study Trials

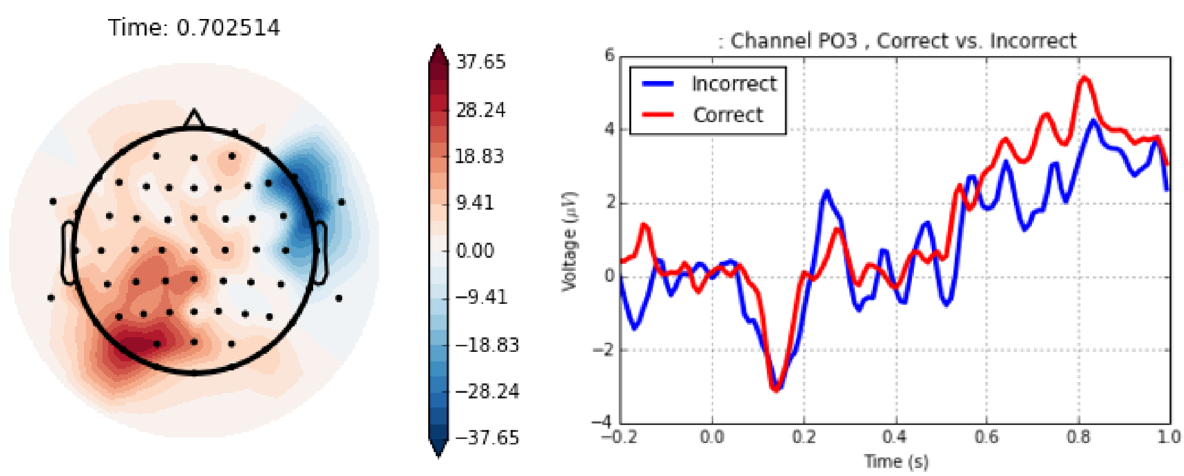

Fig. 5 - ERP at Correct Retrieval of Targets with High Confidence Compared to Lures

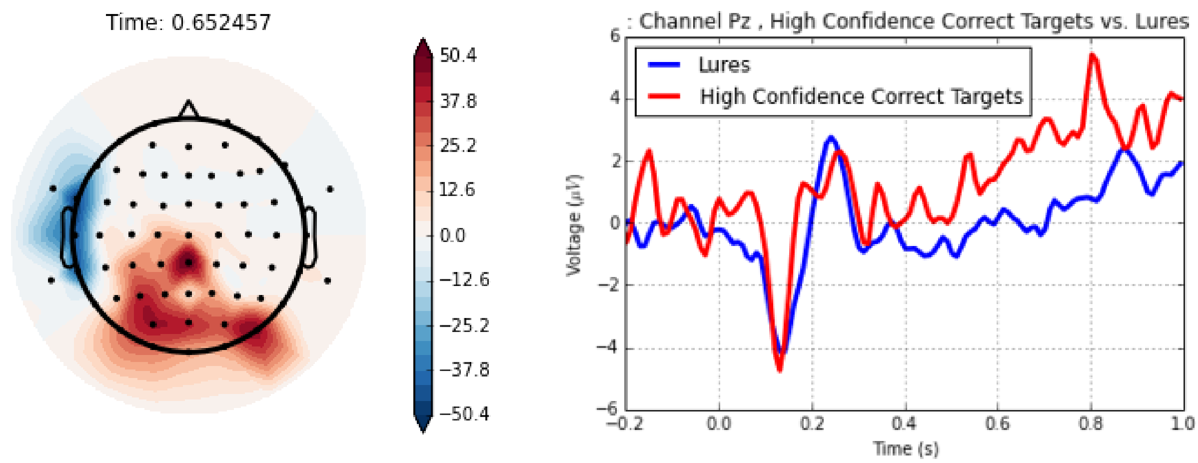

Fig. 6. - Average Pupil Size Across Subjects